

A REVISION OF THE SUBGENUS *NOGUEIRAPIS*;  
AN ARCHAIC GROUP OF STINGLESS BEES  
(HYMENOPTERA: APIDAE)<sup>1</sup>

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RECEIVED FOR PUBLICATION AUGUST 22, 1962

ABSTRACT

*Nogueirapis* represents a natural group of the genus *Trigona* and is regarded as a valid subgenus. Three species, *butteli*, *mirandula*, and *silacea*, this latter a fossil from the Middle Miocene amber of Chiapas, Mexico, are included in this subgenus. The affinities of subgenera are discussed, the evolution of the subgenus is considered, and the species are redescribed. The two living species are so similar, structurally, to the fossil one that they may be considered indirect descendants.

The subgenus *Nogueirapis* was erected by Moure in 1953 to include the species described by Friese as *Trigona butteli*, an apparently rare form from South America. Since the subgenus *Nogueirapis* was described (Moure, 1953), two more species have been included: (1) *Trigona mirandula* Cockerell, a rare species from Costa Rica and Gorgona Island, Colombia, that has passed unnoticed for more than forty years. It was rediscovered by Moure in 1959 when studying types and (2) *Trigona silacea* Wille, a fossil bee from the Middle Miocene amber of Chiapas, Mexico, described by the author (Wille, 1959). The similarity of the fossil form to the two living species is so close that it is possible that *T. mirandula* and *T. butteli* are indirect descendants from the fossil. The purpose of the present paper is to show this relationship and the possible phylogenetic arrangement of the species. Redescriptions of the species are also given. New descriptions have been greatly needed for *T. mirandula* and *T. butteli*, which were poorly described. As to *T. silacea*, new and better material was made available to the author, which helped in making a few minor corrections in the original description of *T. silacea*.

1. This study was aided by a grant from Sigma Xi.
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Males and queens of these bees are unknown. However, there is one male among the fossil material that could be assigned to *Nogueirapis*. Unfortunately, the fossil is not well preserved, and it seems advisable at present to await further studies. The wing terminology follows that of Michener (1944).

#### COMMENTS ON THE GENERAL CLASSIFICATION OF THE STINGLESS BEES

Since *Nogueirapis* was erected by Moure as a subgenus of *Partamona*, a few remarks on the general classification of the stingless bees seem necessary. On the basis of morphology and biology, the stingless bees form a natural group in the subfamily Apinae. Notwithstanding important similarities, they are a diversified group, as might be expected in view of the number of included species, their wide geographic distribution, and their fairly long geological history. The need to divide them into different categories was early felt by several investigators. These groups have been given different taxonomic rank by various writers, and the number of genera and subgenera accepted has varied according to the authors. In the study of the group *Nogueirapis* the author has retained a more conservative view. Except for the genera *Lestrimelitta*, *Dactylurina*, *Meliponula* and *Melipona* there are advantages in retaining the stingless bees in a single genus, *Trigona*, instead of dividing them into some 32 genera. They have essentially similar biologies, and are similar in appearance and basic morphology, in spite of the differences which exist. In its broad sense here used, *Trigona* has a meaning to entomologists and biologists generally which is lost if the genus is dismembered.

In view of the fact that *Nogueirapis* represents a natural group among *Trigona*, it is regarded here as a valid subgenus. Its affinities are discussed in a special section below.

#### THE SUBGENUS *NOGUEIRAPIS*

##### Subgenus *Nogueirapis* Moure

*Nogueirapis* Moure, 1953, *Ciencia e Cultura*, S. Paulo, v. 5, No. 4, p. 247.

Type species: *Trigona butteli* Friese, 1900 (by original designation and monotype).

DIAGNOSTIC CHARACTERS The subgenus *Nogueirapis* can be easily

recognized from any other group of stingless bees by the combination of characters 2, 8, 10, 18 and 22 below. The characteristic black spot on the frons and vertex, plus the black distal area of the hind tibia can be used as an easy and quick way to separate them from other bees. Characters are:

1. Small to medium size (3 to 5 mm. in length).
2. Body ferruginous with dark markings which consist mainly of large bilobed area on upper part of head (Fig. 1), distal area of hind tibia (Fig. 2, A to C), hind basitarsus, and distal border of each abdominal tergum.
3. Cuticular surface smooth and polished with punctation very sparse and delicate.
4. Anterior width of head 1.2 times anterior length.
5. Antennal sockets perceptibly below middle of face and immediately above epistomal suture, so that length of supra-antennal area is twice length of infra-antennal area.
6. Subantennal sutures absent.
7. Scape not reaching anterior ocella.
8. Interantennal space 1.7 times width of flagellum.
9. Lateral portions of epistomal suture almost straight and diverging anteriorly.
10. Width of clypeus about twice its length.
11. Length of malar space less than width of flagellum.
12. Preoccipital carina absent.
13. Mandibles bidentate on inner apical margin.
14. Length of pronotum twice width of flagellum.
15. Width of mesoscutum 1.1 times its length.
16. Mesoscutellum short but extending backwards slightly, just covering mesal portion of metanotum as seen from above, and with apex rounded.
17. Width of mesoscutellum about twice its length.
18. Distance between lower metapleural suture and second coxa less than width of flagellum.
19. Basal area of propodeum glabrous.
20. Hind tibia subtriangular to subclaviform, with posterior distal extremity rounded, at most slightly angular.
21. Corbicula occupying slightly more than half of tibia.
22. Posterior margin of hind tibia with simple hairs only.
23. Inner surface of hind tibia uniform, without a depression along the posterior border. (In *T. silacea* there is an apparently median elevation which seems to leave a posterior flange or depression; however, the apparent depression is differentiated only by its dark coloration and lack of hairs, and not by an actual elevation.)
24. Length of basitarsus about twice its width.
25. Sides of basitarsus subparallel, with posterior angle slightly projected.
26. Inner surfaces of basitarsus uniformly covered with bristles.
27. Pterostigma relatively narrow, its length about four times its width.
28. Submarginal angle (between  $R_s$  and  $R_s+M$ ) right angular to slightly more than  $90^\circ$ .
29. Hind wing with 5 hamuli.
30. Jugal lobe slightly less than one half as long as vannal lobe.
31. Abdomen relatively short and wide, subtriangular, with dorsal surface slightly convex.

**DISTRIBUTION** This subgenus is restricted to the American continent. *T. silacea* is found in Mexico; *T. mirandula* in Costa Rica and Gorgona Island, and *T. butteli* in Brasil, Perú and Bolivia.

**AFFINITIES** The exact position of *Nogueirapis* is still uncertain. Indications are that this subgenus is a primitive group. This is shown by its long geological history and by its unspecialized gen-

eral morphology. Unfortunately, the chromosome number, nest structure, and communication system are at present not known; such data would help to evaluate its level of primitiveness. On the basis of its unspecialized morphology and general appearance, the subgenus *Plebeia* appears close to *Nogueirapis*. However, *Plebeia* differs from it by the possession of a narrow depression along the posterior border of the inner surface of the hind tibia. The similarities of *Nogueirapis* and *Plebeia* are so striking that if the former had the narrow depression in the hind tibia there would be little hesitation by a bee specialist in placing the bees that we are now grouping as *Nogueirapis* in the subgenus *Plebeia*. Moure (1953) has placed great emphasis on the nature of the inner surface of the hind tibia, and has distributed phylogenetically all the stingless bees in three major groups: (1) bees which have the inner surface of the hind tibia normal, without any type of depression, (2) bees with a narrow depression along the posterior border of the inner surface of the hind tibia, and (3) bees with a wide depression along posterior area of the inner surface of the hind tibia which widens at its apex. Since the hind tibia of most stingless bees has another small depression or face along the anterior region of the tibia, the bees of this third group appear to have a median elevation along the whole length of the tibia. Since *Nogueirapis* belongs to the first group and *Plebeia* to the second one, Moure has not placed *Nogueirapis* close to *Plebeia*, in spite of the fact that they are similar in other respects. Therefore, *Nogueirapis* has been placed among the bees of group 1. Unfortunately, most bees of this group (*Partamona*, *Paratrigona*, *Scaptotrigona*, and *Nannotrigona*) are, in spite of the unspecialized inner surfaces of the hind tibia, highly specialized in many other respects. *Partamona*, however, is less specialized than *Paratrigona*, *Scaptotrigona*, and *Nannotrigona*. This is the reason why Moure has placed *Nogueirapis* close to *Partamona*, as a subgenus of it. But since there are some important differences between *Nogueirapis* and *Partamona*, there seems little justification for placing them together. *Partamona* differs from *Nogueirapis* mainly in the epistomal suture, the lateral portions of which are subparallel over their basal halves or more and then diverge abruptly in apical halves; in the propodeum, in which the basal area is covered with hairs; in the hind tibia, which is spoon-shaped; in

the corbicula, which is large; and in the malar space, which is larger. All these characters are presumably specializations, not found in *Nogueirapis*. But if we accept the nature of the inner surface of the hind tibia as one of the main phylogenetic trends in the stingless bees, then the group *Nogueirapis* is at the very bottom of the series of bees with normal inner surfaces of hind tibiae. Similarly *Plebeia* seems to be at the bottom of the series of bees with a narrow depression along the posterior border of the hind tibia. This situation may explain why *Plebeia* and *Nogueirapis* are morphologically similar, even if they are not in the same line of evolution.

Key to the species of *Nogueirapis*

1. Fossil; length of body 3 mm.; base of first median cell petiolated  
*silacea* Wille
- Living length of body 5 mm.; base of first median cell non-petiolated ... 2
2. Mesoseutum black; rastellum composed of 8 strong bristles  
*mirandula* Cockerell
- Mesoseutum ferruginous; rastellum composed of 9 strong bristles  
*butteli* Friese

*Trigona (Nogueirapis) silacea* Wille

*Trigona (Nogueirapis) Silacea* Wille, 1959, *Journal of Paleontology* 33, No. 5, p. 849.

SIZE Length 3 mm.; length of forewing 2.7 mm.

COLOR General color ocher or ferruginous. A large bilobed dark spot on upper part of head (Fig. 1, A), covering vertex and extending anteriorly about two thirds of supra-antennal area, to level above antenna, where black is excavated medially around frontal line, excavation narrow and more or less triangular in shape, not reaching anterior ocellus, separated from it by a width which is slightly more than twice width of flagellum; lower ends of spot gently curved and at sides gradually curved upwards leaving narrow ocher paracocular area; posteriorly, black spot extends to same level as anteriorly. Other dark areas: dorsal surface of flagellum; distal margin of mandible and narrow strip at base; malar area; scutellum, metanotum, inner and outer sides of posterior (one fourth) and distal (one sixth) border of hind tibia (Fig. 2, A); hind basitarsus; distal border of each abdominal tergum, thus forming a series of five (the sixth slightly indicated) black bands, each band as wide as width of flagellum.

STRUCTURE Length of eye 2.2 (2.3) times breadth; length of malar space slightly less than (.85) width of flagellum; anterior border of pronotum slightly concave; distance between lower metapleural suture and second coxa one third width of flagellum; length of propodeal spiracle 3.3 times its width; shape of hind tibia subtriangular (Fig. 2, A), with posterior distal angle rounded; length of hind tibia 2.5 times its width; without well

defined corbicular hairs (long hairs found sometimes on the corbicular surface), rastellum composed of 10 to 14 long hairs slightly longer than width of flagellum; hairs of inner surface of hind tibia confined to median region, leaving posteriorly a wide glabrous margin (almost as wide as flagellar width); forewing with following veins usually weakly indicated: Cu, Cu<sub>1</sub>, Cu<sub>2</sub>, 1st m-cu, and following abscissae of M; submarginal cells virtually absent; but sometimes weakly indicated; length of marginal cell 3.6 times its width; submarginal angle (basal angle first R<sub>1</sub> cell) about 90°; base of first median cell petiolated (Fig. 2, D).

VARIATION There are some variations in the color of the fossil forms. Some of these differences are obviously due to the direction of light in the amber. Thus, the dark areas may appear either black or brown.

Other minor morphological variations can be attributed to the medium of

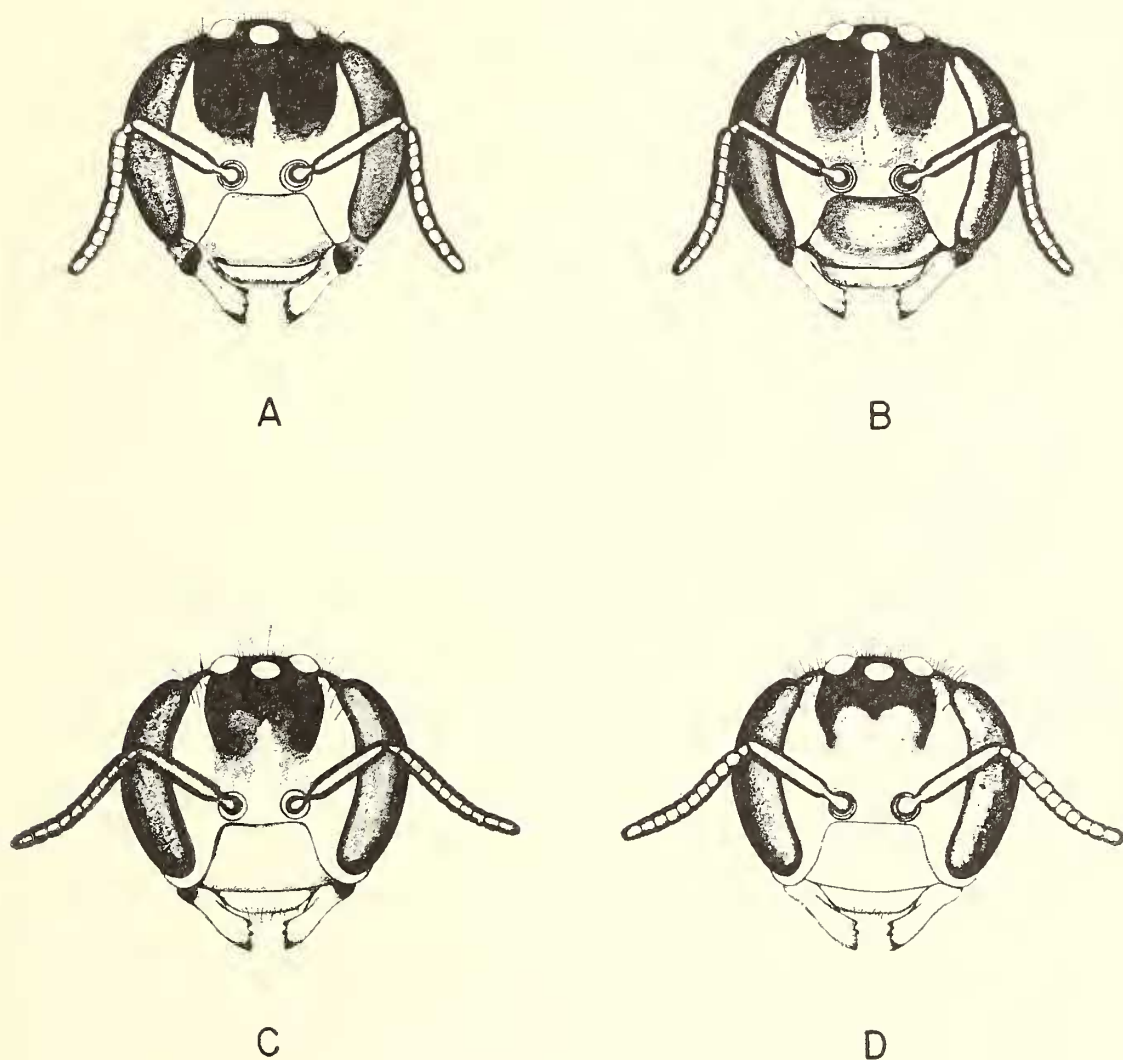


FIG. 1

FIG. 1. Anterior view of head of: A. *Trigona silacea*; B. *Trigona mirandula*; C. *Trigona butteli* (a variant); D. *Trigona butteli*.

preservation, for example, the small variations in the relative lengths of some of the structures may be due to the different pressures exerted by the amber on some of the specimens.

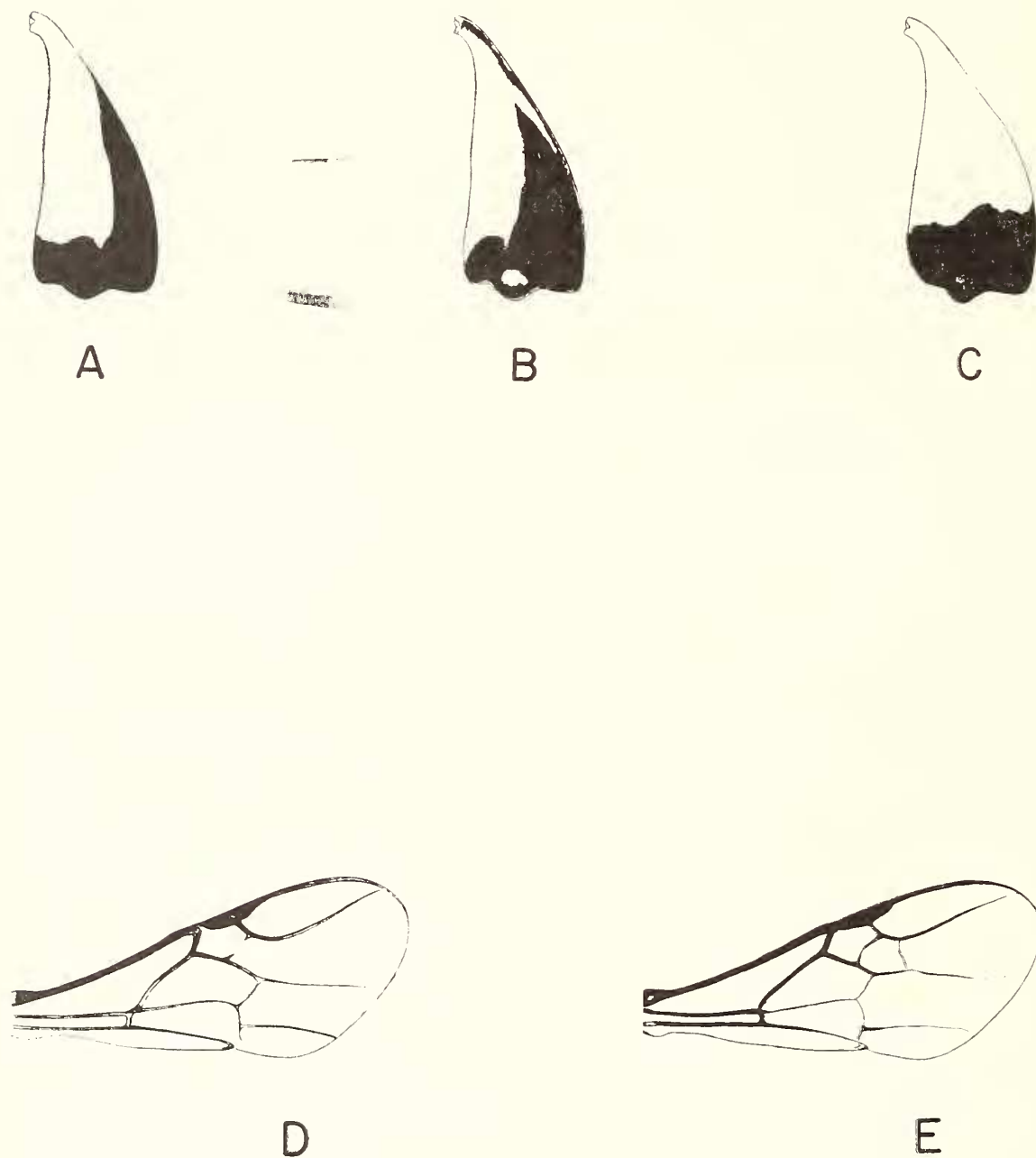


FIG. 2

FIG. 2. Outer surface of left hind tibia and left forewings of *Nogueirapis* (hairs omitted). A. *Trigona silacea*; B. *Trigona mirandula*; C. *Trigona butteli*; D. *Trigona silacea*; E. *Trigona mirandula*.

**DISTRIBUTION** All the specimens known come from Chiapas, Mexico, from two different localities in the vicinity of Simojovel: from Rio San Pedro, opposite town of San Pedro and from the Simojovel landslide.

**TYPE MATERIAL** the holotype No. 12601, and paratypes Nos. 12602–12611 are in the Museum of Paleontology, University of California.

**SPECIMENS EXAMINED** Besides the holotype and paratypes the author has examined a large new series of specimens found recently by the University of California, from the same area.

*Trigona (Nogueirapis) mirandula* Cockerell

*Trigona mirandula* Cockerell, 1917, *Psyche*, 24, No. 4, p. 122.

**SIZE** Length 5 mm.; length of forewing 4.6 mm.

**COLOR** General color ferruginous; distal border of mandible reddish. A large bilobed black spot on upper part of head (Fig. 1, B), covering vertex and extending anteriorly about two thirds of supra-antennal area, to level above antenna, where black is excavated medially around frontal line, excavation narrow, half width of flagellum, and reaching anterior ocellus, but sometimes separated from it by a width equal to that of flagellum, lower ends of spot gently curved and at sides curves upwards and toward eye margin at summit, leaving a wide yellowish paracocular area, much wider than width of flagellum; posteriorly, black spot extends only near upper margin of declivity of posterior surface of head. Other dark or black areas: dorsal distal part of scape; pedicel; flagellum dark brown, slightly paler beneath; around posterior articulation of mandible; mesoscutum; scutellar crest; outer surface of posterior (half) and distal (one fifth) border of hind tibia (Fig. 2, B); outer surface of basitarsus; tarsus almost black; distal border of each abdominal tergum, thus forming a series of five (the sixth slightly indicated) black bands, each band much wider (1.5) than width of flagellum. When the abdomen is contracted, each basal portion of tergum, which is dark ferruginous, is covered by the black distal border of the preceding segment; therefore, the dorsal surface of abdomen may appear as black. The following parts yellowish: paracocular areas; a bottle-shaped area around frontal line, but with a small ferruginous line medially in the wider portion; inter-antennal area, just above clypeus; a very narrow area in anterior portion of clypeus, slightly wider at both extremities (sometimes only the extremities are evident as two yellowish spots); basal half of mandible; scape, except black portion, although sometimes it approaches ferruginous; a narrow genal area along posterior margin of eye; a narrow band along lateral margins of mesoscutum; axillae; basal half or pronotum; posterior lobe of pronotum and metaepisternum appear paler in color, almost ferruginous; wings of a uniform yellowish gray color.

**STRUCTURE** Length of eye 2.5 times breadth; length of malar space slightly less than half (.35) width of flagellum; anterior border of pronotum slightly



concave, almost straight; distance between lower metapleural suture and second coxa one fourth width of flagellum; length of propodeal spiracle 3.8 times its width (measure from inner border of atrial rim); shape of hind tibia subtriangular (Fig. 2, B) with posterior distal extremity slightly angulated; length of hind tibia 2.5 times its width; with a corbicular hair, almost as long as length of scape (there is another long hair, but much shorter than corbicular hair and closer to hind border of tibia); rastellum composed of 8 strong bristles, as long as width of flagellum, and restricted to median area of distal border of tibia; hairs of inner surface of hind tibia uniformly distributed posteriorly, leaving just a very narrow margin glabrous; vein separating first and second submarginal cells (Rs) relatively well indicated, that separating second and third (1 r-m) virtually absent; length of marginal cell 3.8 times its width; submarginal angle (basal angle of first  $R_1$  cell) a right angle; base of first median cell non-petiolated (with vein separating first cubital and median cells transversally placed. Fig. 2, E). VARIATION The main variation found is in the length of the narrow yellowish strip around the frontal line, which usually reaches the anterior ocellus. In some of the specimens, however, the strip does not extend as far as the anterior ocellus, and can be separated from it by a width equal to that of flagellum (Fig. 3, B).

DISTRIBUTION As far as we know this species occurs only in Costa Rica, in a place called Pozo Azul de Acosta, and in Gorgona Island, Colombia. The type locality is Pozo Azul. This place, with an altitude of 82 to 200 meters, is located in the pocket-like area formed by the union of the rivers Rio Grande Candelaria and Rio Pirrís (Parrita). The area is isolated toward the west, south and east by the two rivers, and toward the north by the high mountains of Sabanillas de Acosta (1165 m.) and Serros del Dragón (2505 m.). This species was collected for the first time in June 15, 1909 by M. A. Carriker. During the following 52 years it was not collected again in Costa Rica. Very recently, however, the author has secured a large series of *T. mirandula* during three expeditions to Pozo Azul. So far, the author has failed to collect this bee from any place other than Pozo Azul.<sup>1</sup>

The existence of *T. mirandula* in the island of Gorgona, at present a penal colony, was observed by Moure when studying Chessman's material in the British Museum. According to Moure, in a personal communication, what Chessman (1929) calls *Trigona mosquito* var. *varicolor* from Gorgona Island is

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<sup>1</sup> However, since this paper was submitted for publication, I have collected *T. mirandula* in Rio Damitas, 14.5 Kms. north of Quepos, at the base of the mountains of Dota (altitude 200 m.), province of San José, Costa Rica.

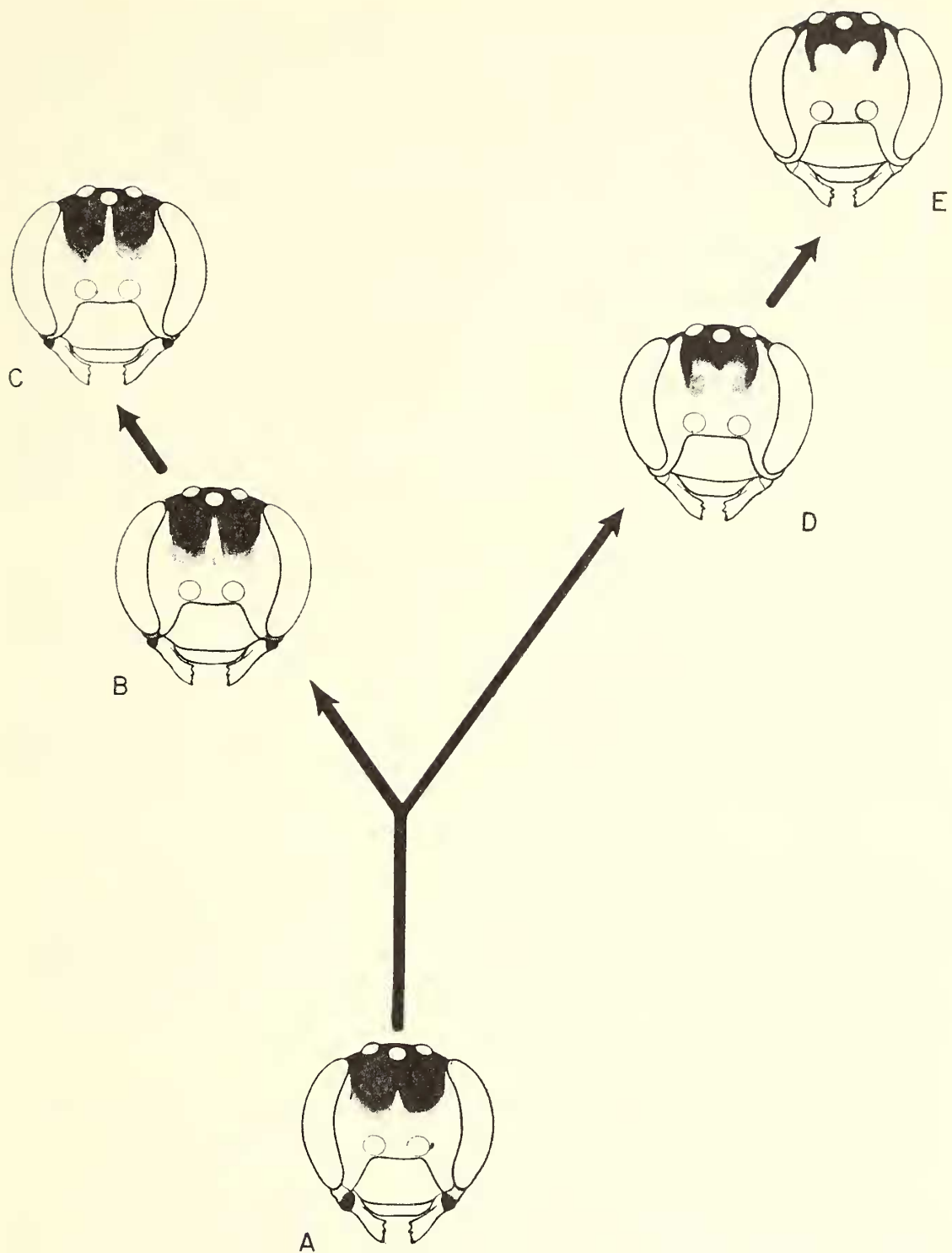


FIG. 3

FIG. 3. Evolutionary trends of the black spot on the frons and vertex in *Nogueirapis*. A. As in *Trigona silacea*. B. As in *Trigona mirandula* (a variant). C. As in *Trigona mirandula*. D. As in *Trigona butteli* (a variant). E. As in *Trigona butteli*.

actually *T. mirandula*, which differs from the type only in very minor things. Since the type of *variicolor* exists, the name *mosquito* var. *variicolor* applied to the bee from Gorgona Island is a misidentification and not a synonym of *mirandula*.

**BIOLOGICAL DATA** Practically nothing is known about the biology of this bee. There is hope that soon the author may be able to carry out some research on its general behavior. The species seems to be strictly a jungle form, not a single specimen has been collected in flowers outside of the forest, not even in areas close to the edge of the jungle. Workers are easily attracted with a solution of honey. The first time they were collected by the author, they were on a fallen tree, where some woody vines had stripped and torn the bark, the bees being attracted to the sap of the wounds.

**TYPE MATERIAL** The holotype No. USNM-23168 is in the U. S. National Museum. A plesiotype worker from Pozo Azul, Costa Rica, is here designated and is being sent to the Snow Entomological Museum at the University of Kansas.

**SPECIMENS EXAMINED** Besides the plesiotype, the redescription has been based on 50 specimens, all from Pozo Azul, Costa Rica.

*Trigona (Nogueirapis) butteli* Friese

*Trigona butteli* Friese, 1900, Természetrájsi Füzetek, 23, p. 393.

*Melipona butteli*, Ducke, 1916, Revisão das Espécies de Abelhas do Brasil, in Comissão de Linhas Telegraphicas Estrategicas de Matto Grosso ao Amazonas, (Publicação No. 35), Anexo No. 5, Historia Natural, Zoologia, p. 33; Ducke, 1916, l.c., p. 100; Ducke, 1925, Zool. Jahrb., Abt. Syst., vol. 49, p. 398.

**SIZE** Length 5 mm.; length of forewing 4.6 mm.

**COLOR** General color pale ferruginous; distal border of mandible reddish. A large black spot on upper part of head around ocelli (Fig. 1, C), extending anteriorly about one half of supra antennal area, where it gradually fades away to brown and pale brown color down to level of antennae, but leaving uncovered a pale ferruginous to yellowish area around base of frontal line, and a wide pale yellowish paraocular area, much wider than width of flagellum. Anteriorly, dark spot fades away unevenly, thus lateral sides of dark area extend down more than general median region, forming two lateral projections (Fig. 1, C); there is also a smaller V-shaped projection along frontal line sometimes weakly indicated. Area between posterior ocelli and eye margin dark brown, that behind it very light brown. Other dark areas: dorsal part of scape; pedicel; dorsal part of flagellum; anterior part of mesoscutum slightly darker; outer surface of distal third of hind tibia (Fig. 2, C); outer surface of basitarsus; distal border of each abdominal tergum, thus forming a series of five (the sixth slightly indicated)

black bands, each band as wide as width of flagellum. The following parts pale yellowish: paraocular areas; around frontal line; interantennal area; most of clypeus, slightly darker at its sides and more yellowish at distal extremities; basal two thirds of mandible; scape, except black portion (occasionally ferruginous); a narrow genal area along posterior margin of eye, sometimes not well indicated; a narrow band along lateral margin of mesoscutum; axillae; basal half of pronotum; wings of a uniform yellowish gray color.

**STRUCTURE** Length of eye 2.2 times breadth; length of malar space slightly more than half (.62) width of flagellum; anterior border of pronotum slightly concave; distance between lower metapleural suture and second coxa one half width of flagellum; length of propodeal spiracle 3.8 times its width (measure from inner border of atrial rim); shape of hind tibia subclaviform (Fig. 2, C) with posterior distal extremity slightly angulated; length of hind tibia 2.4 times its width; with two corbicular hairs, sometimes only one, almost as long as length of scape; rastellum composed of 9 strong bristles, as long as width of flagellum, and restricted to median area of distal border of tibia; hairs of inner surface of hind tibia uniformly distributed posteriorly, leaving just a very narrow margin glabrous; vein separating first and second submarginal cells (Rs) faintly indicated, that separating second and third virtually absent; length of marginal cell four times its width, submarginal angle (basal angle of first  $R_1$  cell) slightly more than  $90^\circ$ ; base of first median cell non-petiolated (with vein separating first cubital and median cells transversally placed).

**VARIATION** The main variation found is in the dark spot on the upper part of head, which may appear with the two lateral projections larger, and resembling more the bilobed condition (Fig. 3, D).

**DISTRIBUTION** The species was originally described from Villcanota, Departamento Cuzco, Perú. It was collected later in Pebas, Departamento Loreto, Perú; in Tarata, Departamento Cochabamba, Bolivia, and Tefé, Estado de Amazonas, Brasil. More recently (1952) it has been collected by Theodore Dobzhansky in the mouth of the river Vaupés (Caiarí), Territory of Rio Negro, Brasil.

**BIBOLOGICAL DATA** none

**TYPE MATERIAL** According to Moure (personal communication) the holotype should be in Friese's collection in the Zoologischen Sammlungen in the Humboldt Universität. Moure saw a "cotypus" from Pebas, Perú, labeled as "typhus" by Friese, in the American Museum of Natural History in New York. A plesio-type worker from the mouth of the river Caiarí (Terr. Rio Negro), Brasil, is here designated and returned to the Snow Entomological Museum at the the University of Kansas.

**SPECIMENS EXAMINED** Besides the pleisotype from Brasil, the re-

description has been based on one specimen from Tarata, Bolivia, and another one labeled simply "Perú, 1900," possibly from Vilcanota.

#### DIFFERENCES AMONG THE THREE SPECIES OF *NOGUEIRAPIS*

The two living forms, *T. mirandula* and *T. butteli*, are closely related species. Not only are they morphologically similar, but the color and general distribution of the dark and yellow marks are almost identical. A comparison between the two species gives the general impression that the color of *T. butteli* is slightly more faded. The obvious difference is the color of the mesoscutum, which is black in *T. mirandula* and ferruginous in *T. butteli*. The other color differences are minor details, all of which are summarized in Table I.

The main morphological differences between the two living forms are found in the proportions of the eye and in certain details of the hind tibia. In *T. mirandula* the compound eye is slightly narrower and larger than that of *T. butteli*; consequently, the malar space is very small in *T. mirandula* and slightly larger in *T. butteli*. The hind tibia is slightly wider in the South American form than in the Costa Rican species, and tends to be subclaviform rather than subtriangular as in *T. mirandula*. There is one well developed corbicular hair in *T. mirandula*, while there are usually two in *T. butteli*. Moreover, the latter species has a rastellum formed by 9 strong bristles, while in *T. mirandula* the rastellum is formed by 8 strong bristles. These morphological differences as well as the minor ones are summarized in Table I.

Although the two living species are similar to the fossil form, there is a larger gap between it and the living forms than between the two living species. These differences are mainly in size, a character in the wing venation and some details of the hind tibia. As to the color, there are minor differences, although nothing is known about the possible yellow marking in the fossil, since the amber would not allow the distinction of such a color.

Of the two living species, *T. mirandula* is more closely related to the fossil form. This is shown in Table I, in which the general color, the anterior view of the black spot on the top of the head, (Fig 1, A, B), the color of the posterior articulation of the mandible, the color of malar space, the distribution of the black color on the hind tibia (Fig. 2, A, B), the shape of the hind tibia

(Fig. 2, A, B), and the submarginal angle of the forewing, are characters which agree in *T. silacea* and *T. mirandula*.

TABLE I

Color and Morphological Differences Among the Three Species of *Nogueirapis*

Characters	<i>T. silacea</i> (fossil)	<i>T. mirandula</i>	<i>T. butteli</i>
General color	ferruginous	ferruginous	slightly pale ferruginous
Yellow markings	Probably present, well defined but not visible in amber		poorly defined
Anterior view of black spot on top of head	bilobed	bilobed	bilobed condition not well defined
Posterior view of black spot on top of head	Extending down to same level as anteriorly	extending only near upper margin of declivity of posterior surface of head	does not extend beyond ocellar area
Color of posterior articulation of mandible	brown to black	black	pale
Color of malar space	dark	dark	pale
Color of mesoseutum	ferruginous	black	ferruginous
Color of scutellum and metanotum	dark	ferruginous, with scutellar crest darker	pale ferruginous
Distribution of black color on hind tibia	posterior (one fourth) and distal (one sixth) borders	posterior (one-half) and distal (one fifth) borders	distal (one third) border
Color of basal area of each abdominal tergum	ferruginous	dark ferruginous	ferruginous
Length of body	3 mm.	5 mm.	5 mm.
Proportions of eye	Length 2.2 (2.3) times breadth	length 2.5 times breadth	length 2.2 times breadth
Malar space	slightly less than (.85) width of flagellum	slightly less than half (.35) width of flagellum	slightly more than half (.62) width of flagellum
Distance between lower metapleural suture and second coxa	$\frac{1}{3}$ width of flagellum	$\frac{1}{4}$ width of flagellum	$\frac{1}{2}$ width of flagellum
Shape of hind tibia	subtriangular	subtriangular	subclaviform
Length of hind tibia	2.5 times its width	2.5 times its width	2.4 times its width
Restellum	10 to 14 long hairs	8 strong bristles	9 strong bristles
Corbicular hairs	without well defined corbicular hairs	with one corbicular hair	with two corbicular hairs (some times with only one)

TABLE I (continued)  
Color and Morphological Differences among the Three Species of *Nogueirapis*

Characters	<i>T. silacea</i> (fossil)	<i>T. mirandula</i>	<i>T. butteli</i>
Hairs of the inner surface of the hind tibia	confined to median region leaving a wide glabrous margin posteriorly (almost as wide as flagellar width)	hairs uniformly distributed posteriorly, leaving just a very narrow margin glabrous	hairs uniformly distributed posteriorly, leaving just a very narrow margin glabrous
Submarginal angle	right angle	right angle	slightly more than 90°
Base of first median cell	petiolated	non-petiolated	non-petiolated

#### POSSIBLE EVOLUTION OF THE SUBGENUS *NOGUEIRAPIS*

The similarity of the two living species to the fossil form suggests that *T. mirandula* and *T. butteli* are survivors of a line of descent from *T. silacea* (Fig. 3). On the other hand, the differences between the fossil form and the two living species indicate the existence, possibly only in the past, of intermediary forms. It is conceivable that all three species are mere branches from a form or from even different closely related species. The existence of the fossil in Mexico, the geographical distribution, and the more or less intermediate position of *T. mirandula*, seem to suggest that the subgenus *Nogueirapis* originated north of Central America, possibly during the Oligocene, when most of Central America was under water. The migration of *Nogueirapis* toward the south was therefore almost impossible up to the Pliocene, when Central America was again a connecting bridge between North and South America. The Oligocene was actually the ideal geological epoch for the stingless bees to evolve. The warm and humid climate and the world-wide distribution of tropical forests during the Oligocene undoubtedly favored their adaptive radiation. However, the stingless bees as a group probably originated during the Eocene, when modernization of flowering plants and development of extensive forests took place. During the Oligocene, Miocene and Pliocene, *Nogueirapis* probably evolved into several species. The first ones were probably small bees, the size of *T. silacea*. Others may have evolved later, in which the capacity for collecting pollen improved. This im-

provement was reflected in the increase of size (corbicular surface), a well developed rastellum, made up of stiff setae, and the appearance of corbicular hairs, which possibly help in holding together the mass of pollen on the corbicula. During the Miocene the species of *Nogueirapis* were probably impelled to migrate south, since the climate in North America started to change greatly, becoming cool and semi-arid. It was also the beginning of forest reduction. In the Upper Miocene Costa Rica emerged again, establishing a connection with Nicaragua, and forming a bridge that could be used by the migrating bees. During the Pliocene the climate continued to grow cooler, with increasing restriction of forests, and the Central American bridge was well formed. Possibly by this time *T. mirandula* was well established throughout Central America, and the migration of the species of *Nogueirapis* continued into South America, where *T. butteli* became well established over much of the continent. The continued coolness of climate and the periodic glaciation during the Pleistocene may have been some of the causes for the extinction of great mammals and many trees, and probably also of several species of *Nogueirapis*, leaving *T. mirandula* and *T. butteli* as the only known survivors of the subgenus.

#### ACKNOWLEDGMENTS

I am indebted to Dr. C. D. Michener of the University of Kansas and Dr. Rafael Lucas Rodríguez of the University of Costa Rica, for reading the manuscript and offering suggestions. I am also grateful to P. D. Hurd of the University of California, for making the fossil material available for study. Also Dr. C. D. Michener kindly sent specimens from the Snow Entomological Museum and Pe. J. Moure provided data on the type material. Mr. William Ramíre and Mr. Guillermo Ulate helped to collect specimens of *T. mirandula*.

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**Taxonomists—Please note**

Genus *Zimmeria* Ruckes preoccupied  
(Heteroptera: Pentatomidae)

In 1958 (Amer. Mus. Novitates, no. 168, p. 20) I erected the genus *Zimmeria* to receive three species of halyine pentatomids, viz. *vivanai* (Kormilev), *stali* (Kormilev), and *bergi* (Kormilev). I have since discovered that this generic name is preoccupied by *Zimmeria* Heinrich 1933 (Mitt. Zool. Mus. Berlin, 19, p. 159) for a species in the Ichneumoninae Hymenoptera. It is therefore necessary that the name *Zimmeria* Ruckes be changed. Since I used this name in honor of my good friend the late Dr. John T. Zimmer, I wish to retain the basic part of it and therefore propose the use of *Zimmerana* in its place.

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